

AN ECOGEOGRAPHICAL ANALYSIS OF THE
DISTRIBUTION OF *ASTER ACUMINATUS*
MICHAX AND *A. NEMORALIS* AITON
(ASTERACEAE: ASTEREA)

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RÉSUMÉ

Certains aspects pertinents de la biologie et de l'écologie de deux espèces d'*Aster* de l'Est de l'Amérique du Nord: *A. acuminatus* (espèce de sous-bois frais), *A. nemoralis* (espèce de tourbière à sphaigne) et de leur hybride *A. × blakei* ont été analysées dans le contexte de leurs adaptations à leurs milieux respectifs. Cette analyse permet de mieux comprendre la distribution géographique actuelle de chacun des taxons en fonction de l'histoire post-glaciaire du nord-est américain et du Québec.

ABSTRACT

Pertinent aspects of the biology and ecology of two north american species of *Aster*: *A. acuminatus* (a forest species), *A. nemoralis* (a sphagnum-bog species) and their hybrid *A. × blakei* are analysed in relation to their adaptations to contrasting environments. This analysis gives a better framework for the understanding of present geographic distribution of the taxa in relation to post glacial events in north-eastern America.

Aster acuminatus Michaux and *A. nemoralis* Aiton are two closely related northeastern North American species. They have been placed traditionally in the artificial section *Orthomeris* of genus *Aster* (Fernald, 1950). However, Semple and Brouillet (1980a) prefer to relate them to subgenus *Doellisgeria*. Their closeness is emphasized by the existence of a natural hybrid, *Aster × blakei* (Porter) House (Pike, 1970; Hill & Rogers, 1973).

These taxa are polycarpic perennials, propagated by elongated rhizomes and anenochorous cypselas. They flower from the end of July to mid-September (Brouillet & Simon, 1979). Pollination is entomophilous and unspecialized: Coleoptera, Diptera, Hymenoptera, Homoptera, and Lepidoptera are frequent visitors. Both species are diploid ($2n = 18$, $x = 9$), and no cytogeographical variation has been found (Nelson, 1966; Hill, 1972, 1976; Hill & Rogers, 1970, 1973; Van Faasen & Sterk, 1973; Semple & Brouillet, 1980b). Although they show distinct flavonoid patterns (Hill & Rogers, 1973), the geographical variation of this characteristic was not studied.

Morphological differences are summarized in Table 1. These traits are closely related to ecological preferences. *Aster acuminatus* is a forest herb, while *A. nemoralis* belongs to Sphagnum bogs and other moist, oxylophytic habitats. *Aster* × *blakei* is found at ecotones between forests and bogs.

The purpose of this paper is to synthesize information from various sources to relate distributional limits with specific ecological factors, and to comment on the post-glacial history of these two species.

METHODOLOGY

We followed the methods of Dansereau and Pageau (1966). First, precise distribution maps are needed. Dot maps are better suited for this purpose since they do not reflect authors' biases (Daubenmire, 1978). The second step consists in comparing the limits obtained with isopleths of biotic and abiotic factors.

Distribution maps already available for these two taxa appeared inadequate for our purpose (Dansereau, 1957; Radford et al., 1968; Pike, 1970; Van Faasen, 1971; Rousseau, 1974). Therefore, we compiled more detailed dot maps. The following herbaria were consulted (acronyms follow Holmgren & Keuken, 1974, and supplements): CAN, DAO, GH, MT, MTJB, MTMG, NY, OAC, QFA (in part), SFS, TRT, WAT. Information was retrieved also from literature (Baldwin, 1958; Erskine, 1960; Marie-Victorin & Rolland-Germain, 1969; Radford et al., 1968; Roland & Smith, 1969; Rousseau, 1974; Van Faasen, 1971). Dr. Rouleau (Université de Montréal) and Dr. Argus (National Museum, Ottawa) respectively made their distribution maps available for Newfoundland and Ontario.

Climatological and other physical data were obtained from the following sources: Anonymous (1957, 1974), Baker (1936), Chapman & Putnam (1973), Damman (1965), Ferland & Gagnon (1967), Grandtner (1966) and Hunt (1974). A list of references regarding biotic factors would be too extensive here: relevant information may be found in the following text.

ECOLOGY

Differences in leaf morphology are shown in Figure 1 and summarized in Table 1.

Table 1. Summary of morphological differences between *Aster acuminatus*, *A. nemoralis* and their natural hybrid

	<i>A. acuminatus</i>	<i>A. × blakei</i>	<i>A. nemoralis</i>
stem diameter	2-4 mm	1.5-4 mm	1-2 mm
Stem pubescence	molliform hairs abundant	molliform hairs present	no molliform hairs, often with glandular hairs
number of leaves	less than 20, distant	20-40	300-100+, crowded
leaf shape	oblanceolate to oval, acuminate	lanceolate to oblong, acute	linear to narrowly lanceolate, ± obtuse
leaf margin	flat, coarsely serrate, ciliate	flat to slightly rolled, serration small to coarse, ciliate to scabrous	recurved, entire, scabrous
upper surface	sparsely hairy	hairy-scabrous	scabrous
lower surface	pilose along veins; glands scarce	more pilose; glands ± abundant	densely pilose to glandular
leaf length and width (larger blade)	1-6 cm; 1-8 mm	4-10 cm; 5-25 mm	5-10 cm; 10-60 mm
inflorescence	lax corymbiform, many heads	corymbiform, many heads	1- capitate or corymbose (2-15 heads)
ray	white	white to pink	pink

Following Fernald (1950) and Pike (1970). See also Table 2.

Aster acuminatus has longer, less numerous leaves. It is adapted to lower light intensities. In woodland individuals, the subverticillate leaf arrangement suggests an optimization of total photosynthetic surface (Brouillet & Simon, 1979). Such an arrangement is frequent in forest herbs (e.g. *Trillium*, *Medeola*, *Trientalis*). Grime (1977) suggested that sciaphytes are adapted more to survival through prolonged periods of low light intensity than to maximizing light interception. It is not clear, however, whether the whorled form (forma *subverticillata* Fernald) of woodland plants represents a genetically fixed "ecotype" or a phenotypic variant, as opposed to the typical form with its more regular leaf distribution along the stems.

Conversely, the small, ericoid, numerous and crowded leaves of *Aster nemoralis* suggest an adaptation to strong irradiance and/or other physiological stresses, like a waterlogged, low pH, cool substrate. These characteristics could represent also an adaptation to nutritionally-deficient conditions (Small, 1973; Grime, 1977; Brouillet & Simon, 1979). Intense intra-stratum competition forces this species to shed its lower leaves, after reassimilating vital nutrients (Moore & Bellamy, 1974; Bradbury & Hofstra, 1977). No such shedding was observed in *A. acuminatus*, which is subjected to lower levels of competition.

HABITAT AND DISTRIBUTION

Aster acuminatus Michaux—This species was classified by Dansereau (1957) and Rousseau (1974) as an appalachian element (Figure 2). Its distribution follows the Appalachian Mountains from Rabun County, Georgia, northeastward to southwestern Pennsylvania. There is a gap in central Pennsylvania and Maryland. It is then continuous from eastern Pennsylvania and northern New Jersey northward to eastern Ontario, the Laurentian Hills of Québec, Lac St-Jean, Haute Côte-Nord, Gaspé and the Maritimes. Disjunct populations occur in the Iles de la Madeleine, southwestern Newfoundland, and the eastern end of Lake Erie (south-east Ontario and adjacent New York). A report for Anticosti is not confirmed (Marie-Victorin & Rolland-Germain, 1969). This species is rare in Ontario (Argus & White, 1977), Newfoundland (Damman, 1965), and Georgia.

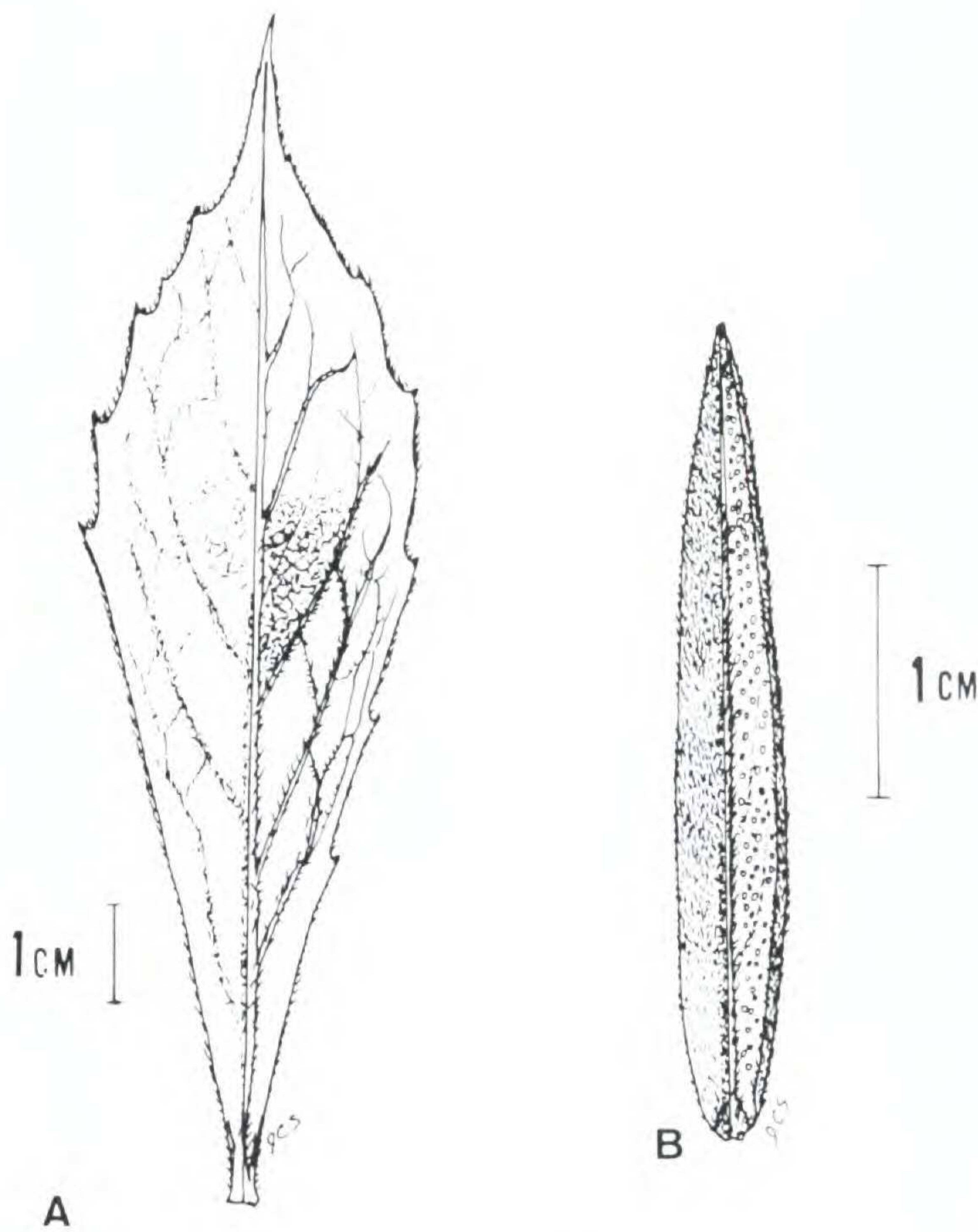


Figure 1. Leaf shape in *Aster acuminatus* (A) and *A. nemoralis* (B). Left side represents upper surface, right side represents lower surface. (Drawings courtesy of Dr. J. C. Semple).

Aster acuminatus inhabits cool forests of northeastern North America. In the mixed mesophytic forest region, it is associated with red spruce at the higher elevations of the Alleghenys. It is commonly found within northern hardwood forests in the oak-chestnut forest region, and becomes a frequent element in the hemlock-white pine-northern hardwoods forest region (Braun, 1950). The limits of these two regions coincide with the southern boundary of *A. acuminatus* range, except in their northwestern part.

Further north, Pike (1970) reports it from moist or mesic coniferous forests in New England and the Maritimes (acadian forest region of Rowe, 1972). Similarly, protected coniferous forests

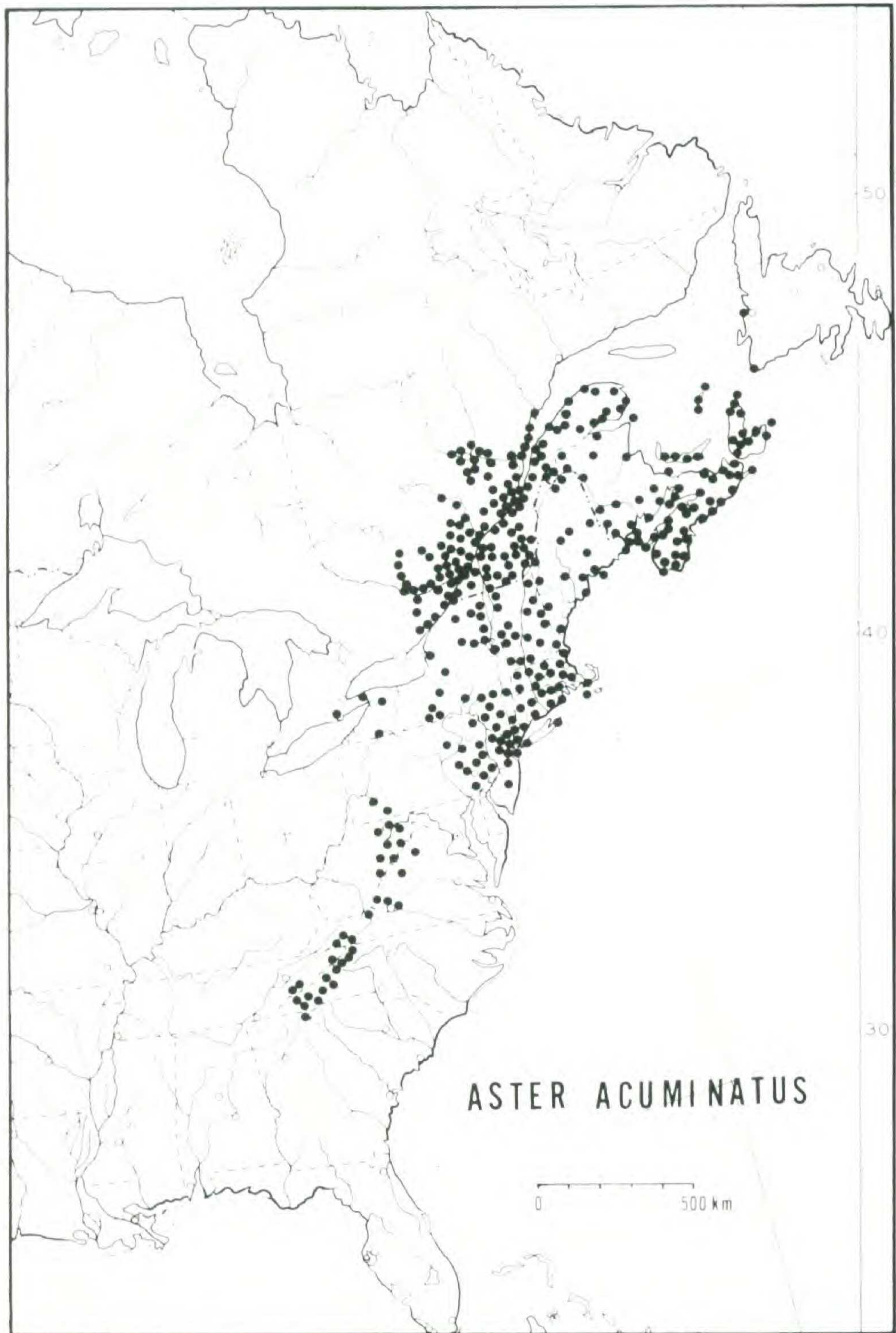


Figure 2. **Distribution of *Aster acuminatus* Michaux** in eastern North America (black dots; empty circles represent major cities).

shelter it in Newfoundland (Damman, 1965). In Nova Scotia, it colonizes also deciduous forests, clearing and woods' edges (Roland & Smith, 1969).

In central Canada, it is found in the eastern sections of the Great Lakes—St. Lawrence forest region (Rowe, 1972). In Québec, it occurs in a variety of forest associations: hickory-sugar maple, laurentian maple, yellow birch-sugar maple, and yellow birch forests, as well as some red spruce or yellow birch-balsam fir forests of the summits of Appalachian hills and Laurentian hills, respectively (Dansereau, 1957; Dansereau & Pageau, 1966; Grandtner, 1966; Bouchard, 1970; Payette & Lavoie, 1971; Op de Beeck, 1972). Its northern limit corresponds to yellow birch-sugar maple forest's northern boundary. We frequently observed it in laurentian maple forests and successional white birch forests in St. Hippolyte (Terrebonne County, Québec), but never on granitic outcrops where white pine predominates. In Repentigny (L'Assomption County, Québec), it was present in a well-drained, cool laurentian maple wood with yellow birch, while it was absent from a lower (by 2m), moister hickory-sugar maple wood. Interestingly, it was also associated with *Trillium undulatum*, a species replaced in the lower forest by *T. grandiflorum*, of more southern affinity. It was also observed in a few moister cedar swamps bordering bogs in St. Hippolyte, an observation corroborated by Gauthier & Grandtner (1975) studies in the lower St. Lawrence region.

Thus, there appear to be two main factors controlling *Aster acuminatus* distribution: 1) reasonably cool, humid areas; 2) good soil drainage. Bouchard (1970) and Op de Beeck (1972) establish that its maximum frequency is in the mesic segment of the moisture gradient, confirming our observations. This explains the irregular occurrence of this taxon in the St. Lawrence lowlands of southwestern Québec and eastern Ontario. The presence of fine-textured, clay soils, particularly in the clay plains of eastern Ontario (Chapman & Putnam, 1973) could be an important factor. On these lowlands, *A. acuminatus* seems to be confined to areas of morainic deposits. The coarse-textured, dry sandy soils of the outwash plain of western Ottawa valley, which support *inter alia* extensive jack pine stands, are likewise inhospitable for this species and act as a barrier to westward migration. A need for acidic substrate (or for a low calcium content) could also play a role at its western limit in Ontario, where substrate is made of limestone.

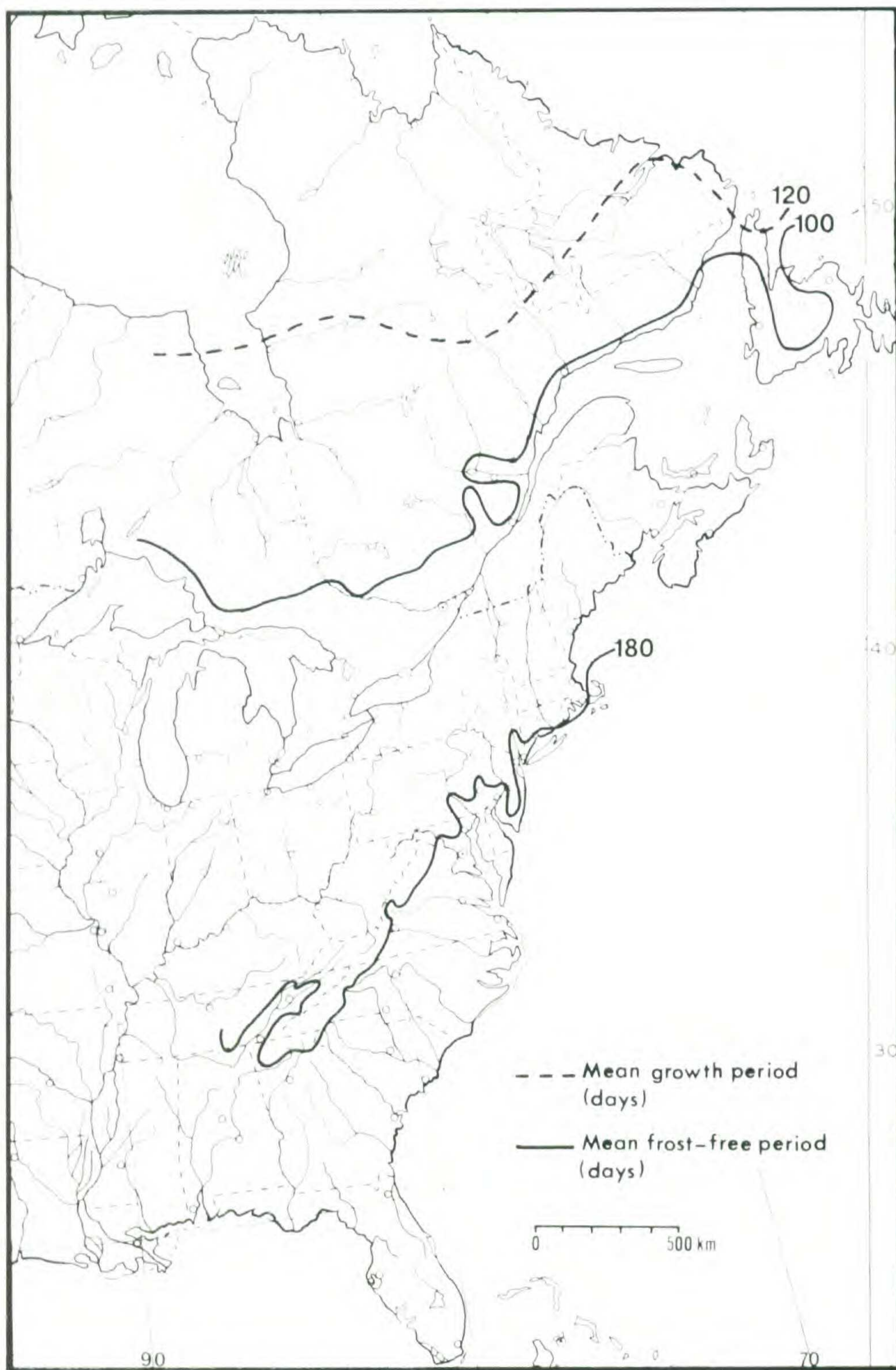


Figure 3. **Isopleths of frost-free period and growth period** (these two climatic parameters are not equivalent) in eastern North America.

At a larger scale, the same factors control its distribution. The impact of the Appalachian Mountains on climate in the south is of major importance. Figures 3 and 4 illustrate this point: frost-free period of 180 days, mean summer and mean July temperatures of, respectively, 21° C and 24° C follow their contour. These parameters coincide closely with *Aster acuminatus*' southern limit. A decrease in humidity could be responsible for the western limit.

The gap in distribution in central Pennsylvania seems also to be related to moisture factors. The mountains are lower and covered with drier forest types (oak, pine). Furthermore, the Piedmont region of Maryland consists of a lower, gently rolling landscape where oaks and hickories are dominant (Braun, 1950). These formations, established on dry soils, seem also unsuitable for the survival of *Aster acuminatus*.

A frost-free period of 100 days (Figure 3) and a mean August temperature of 10° C (Figure 4) are two of many parameters that correlate with the northern range limit (Ferland & Gagnon, 1967). The length of the growing season could play a prominent role, the plant requiring a minimum amount of time to complete its life-cycle. Damman (1965) shows that *Aster acuminatus* on Newfoundland's west coast occupies only a few protected localities where the growth period is warmer and longer and where temperature variations in the spring are less extreme.

Aster nemoralis Aiton—This species has a more northern distribution (Figure 5). It was included among the elements restricted to northeastern North America by C. Rousseau (1974). It ranges from the New Jersey's Pine Barrens to eastern James Bay and Quebec's Basse Côte Nord, and from eastern Lake Superior to the Maritimes and Newfoundland. Disjunct populations occur in central Labrador (northern limit, Rousseau, 1974) and on Anticosti Island. It is rare in Michigan's Upper Peninsula (Wagner et al., 1977) and New Jersey, where its habitat has been severely reduced (Robichaud & Buell, 1973).

Aster nemoralis inhabits characteristically true bogs, *sensu* Dansereau & Segadas-Vianna (1952): blocked drainage, *Sphagnum* mat, organic and acidic substrate, with dominance of Ericaceae, etc. Our observations in St.-Hippolyte lead us to believe that it is a member of the *Caricetum rostratae* (Dansereau & Segadas-Vianna, *loc. cit.*) in southern Québec, a pioneer zone where *Carex*

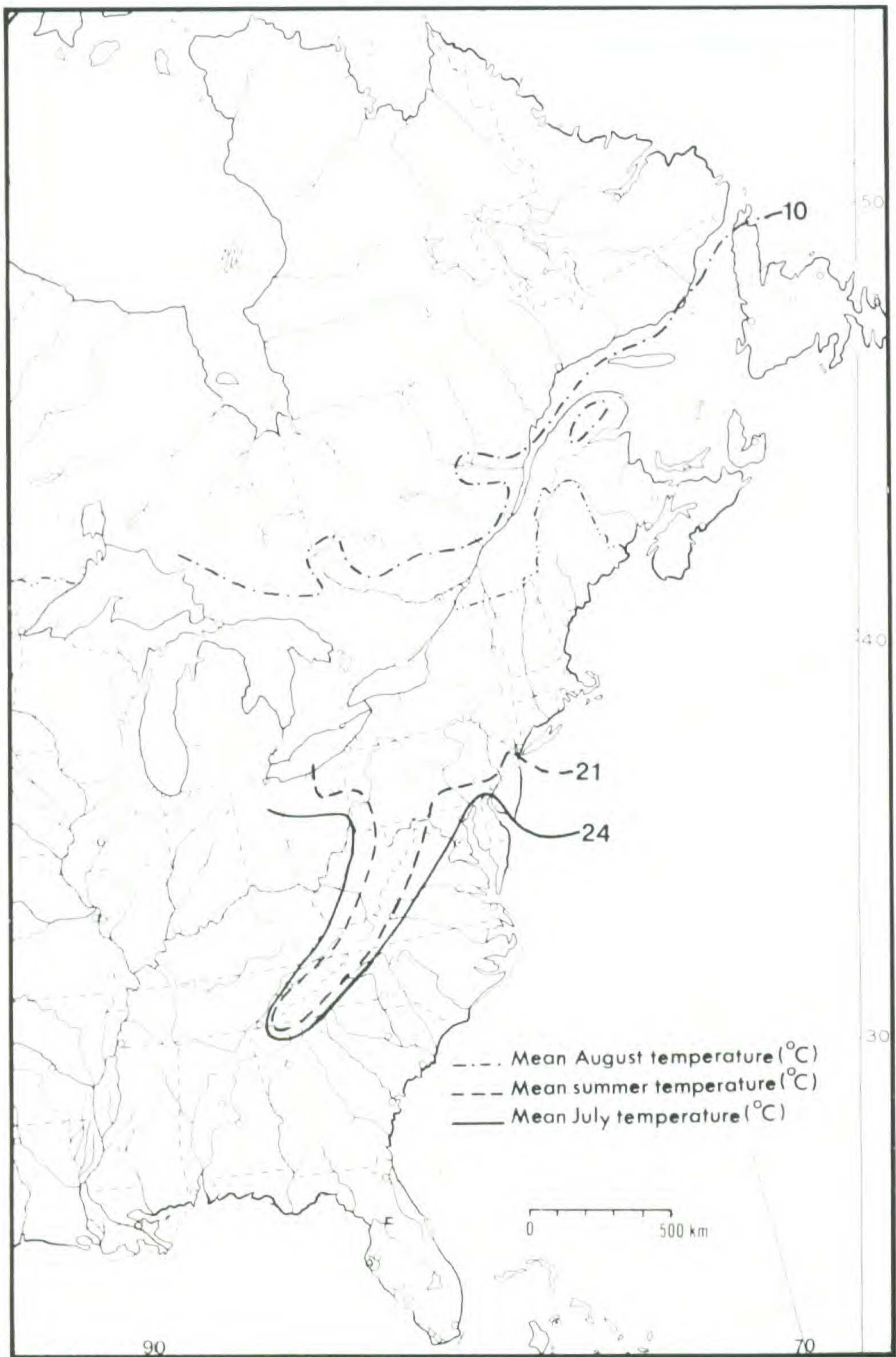


Figure 4. Isotherms in eastern North America.

dominates, with invasion of ericaceous shrubs like *Chamaedaphne calyculata* and *Andromeda glaucophylla*. In Abitibi (Québec), Gaudreau (1975) reports it from a similar association: *Sphagno-Chamaedaphnetum calyculatae*, subassociation *Myricetum galio*, *Carex rostrata* variant. It was not found in similar associations of the Lower St. Lawrence region (Gauthier & Grandtner, 1975), an area where the species becomes rather infrequent. In New Jersey, it colonizes acidic bogs of poorly drained areas in the Pine Barrens (Stone, 1911; Robichaud & Buell, 1973). It occupies similar habitats in Newfoundland (Bouchard, Hay & Rouleau, 1978). However, an organic substrate is not essential. It was thriving along with many other bog elements, in a water-saturated sandy beach of a lake in Parry Sound District (Ontario), not far from a bog in formation. It is unaffected by salt spray in Nova Scotia's coastal bogs (Rousseau, 1938).

The northern limit of the range of *Aster nemoralis* corresponds *grosso modo* with that of the boreal forest, as delimited by Rowe (1972). A length of the growing season of 120 days (Figure 3) (it does not correspond exactly to frost-free period!) could be playing the same role as with *A. acuminatus*. Another factor that may act as a barrier northward is the presence of permafrost (Rowe, 1972).

The close ties between this species and its bog habitat gives us further clues to understand its distribution. Three factors are involved: 1) availability of impoundments; 2) cool, moist climate; and 3) acidic substrate (or low calcium content). The Wisconsin glaciation favored the creation of countless lakes, ponds, and marshes, many adequate for bog development. With the exception of New Jersey, the entire range of *Aster nemoralis* lies within the limits of Wisconsin glaciation (Figure 6). South of this glaciated region, higher temperatures and inadequate geological conditions do not favour this type of bog development (Moore & Bellamy, 1974).

Finally, acidic substrate plays a key role in shaping *Aster nemoralis*' range (Figure 6). It correlates closely with the metamorphic rocks of the Canadian Shield and the Adirondacks. Outside of this formation, *A. nemoralis* is present mostly in regions of acidic bedrock: New England, parts of the Eastern Townships (Québec), the Maritimes and Newfoundland. On Anticosti Island, the only location of this species is Sand-Top, where a bog overlies thick sandy terraces in an area otherwise dominated by limestone

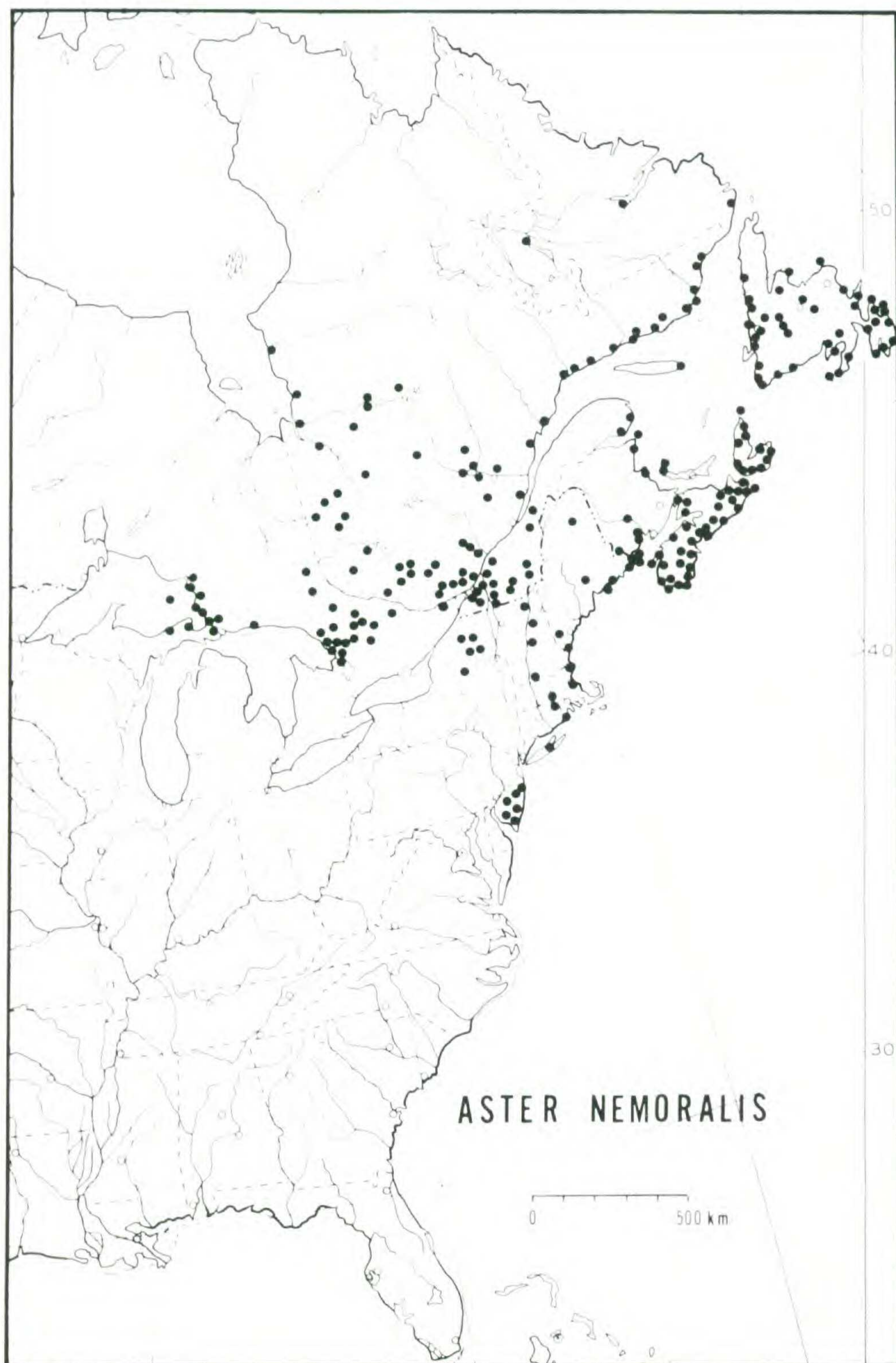


Figure 5. **Distribution of *Aster nemoralis* Aiton** in eastern North America (black dots; empty circles represent major cities).

(Marie-Victorin & Rolland-Germain, 1969). The high calcium content of soils of the area north of Lake Huron (Rowe, 1972) and the Ontario part of the Clay Belt (Baldwin, 1958) could explain the distribution gap observed in this region. The absence of this taxon from the Hudson Bay Lowlands (Figure 6) and Manitoulin Island (Morton, 1977) is also symptomatic.

Aster × **blakei** (Porter) House—Hybrid populations are scattered throughout the area of overlapping of the two parents (Figure 7). They occur wherever ecological conditions foster contact between the parental taxa, mostly at the bog-forest ecotone where tall shrubs like *Myrica gale* and *Nemopanthus mucronatus* dominate. The hybrid often survives today in areas where one parent is absent (Pike, 1970).

The population structure was determined for many sites at St.-Hippolyte (Terrebonne Co., Québec) (Figure 8). We used the index designed by Pike (1970), following the methods of Anderson (1949). Table 2 summarizes the characters used, the value of their different states, and the scores of the various entities. As noted by Pike (1970) and Hill and Rogers (1973), the distribution deviates toward *Aster nemoralis*. A greater success of crosses made using the latter taxon as female parent, as well as the greater similarity between the bog and the ecotone where *A. × blakei* survives, could explain this feature (Hill & Rogers, 1973). Figure 8 (A, C) also shows that even in a sympatric area, and at a local scale, the parent populations maintain their integrity when ecologically isolated. We were unable to find signs of introgression, at least in using this morphological index.

POST-GLACIAL HISTORY

The absence of macrofossils, and the impossibility of distinguishing specific tubiflorae Composite pollens leaves no alternative but circumstantial evidences to reconstruct the post-glacial biogeographical history of these two taxa. Two kinds of data are relevant in this context. First, the history of revegetation after ice retreat, as recorded in radio-carbon dated pollen sequences. Second, fossil and present distribution of plants showing ecological and biogeographical affinities. The discussion presented below is speculative, but nevertheless provides a model that could eventually be tested with the aid of direct fossil evidences.

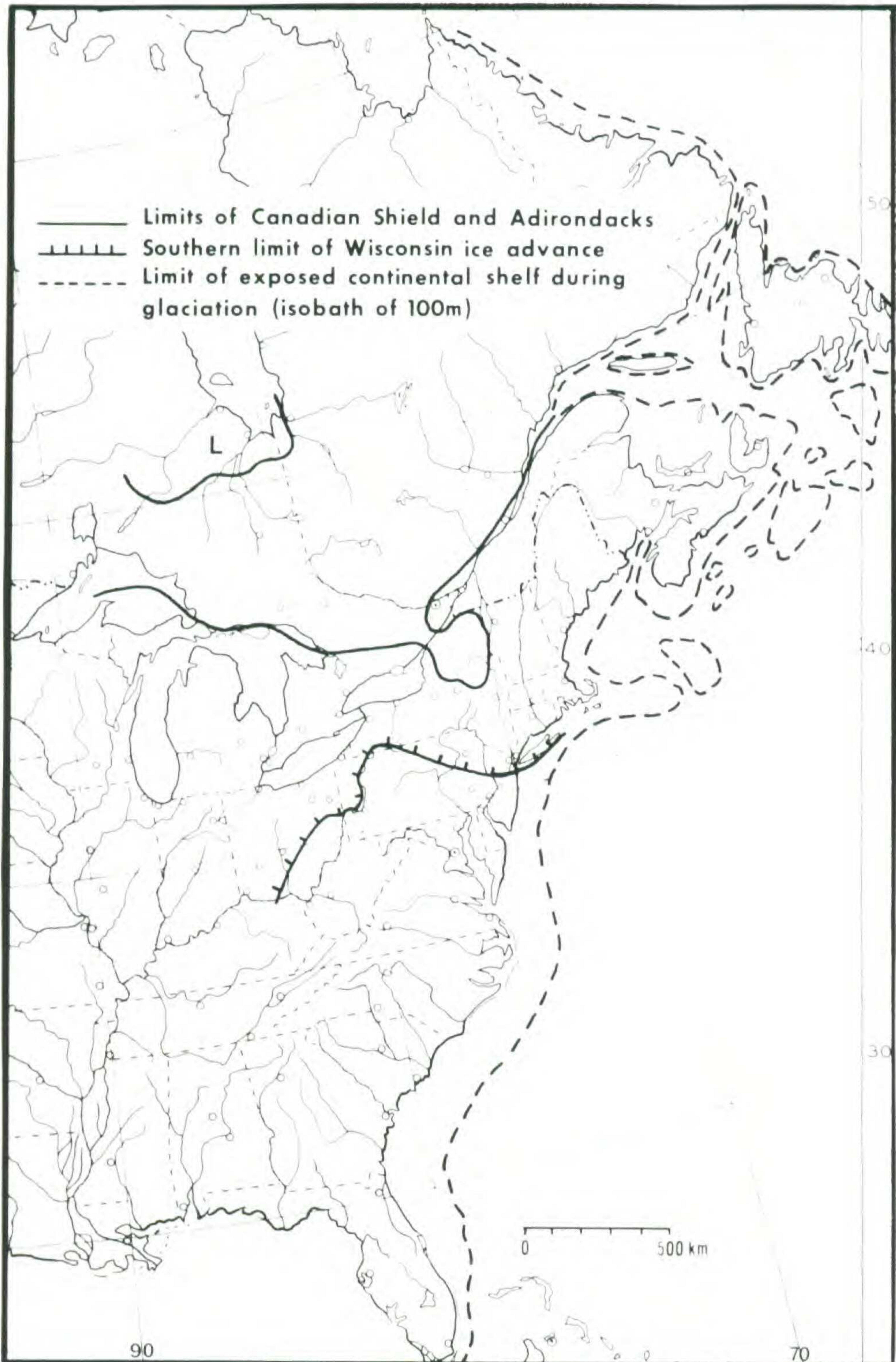


Figure 6. **Past and present geographical factors** in eastern North America. L = Hudson Bay Lowlands. The 100 m depth contour has been redrawn from Flint (1971) and Ogden (1977).

Table 2. Hybrid index of Pike (1970).

Character	Character state value						
	0	1	2	3	4	5	6
number of leaves	100±35	34-32	31-29	28-26	25-23	22-20	19-
ratio leaf length/width	10-7	7-5	<5-4	<4-3.33	<3.33		
internodes length (mm)	1-8	9-11	12-14	15-18	19-23	24-30	
degree of revoluteness	revolute	±revolute	±flat	flat			
degree of scabrosity	scabrous	intermediate	hairy				
leaf serration	entire	tip gland	small	big			
number of bracts/peduncle	4+	3	2	1-0			
number of heads/inflorescence	1	2+					
ray colour	pink	trace	white				
1 zebra hair on stem (molliform)	absent	occur	abundant				

Individuals with total score of 0-4 are assigned to *A. nemoralis*, 8-19 to *A. × blakei*, 25-31 to *A. acuminatus*.

During the last (Wisconsin) glacial maximum (ca. 20,000 yrs B.P.), ice covered entirely northeastern North America (Figure 6). Tundra covered a belt south of the ice front, particularly in Pennsylvania and central New York State, stretching southward along the Appalachian Mountains for a few hundred kilometers. A spruce forest covered most of eastern North America, at least from Georgia northward. At the same time, a spruce- (jack) pine forest occurred on the Atlantic coastal plain. Substantial areas of the continental shelf, to a depth of ca. 100 m below present sea levels (Figure 6) were available to colonization by animals and plants (Flint, 1971; Davis, 1976; Ogden, 1977). *Aster acuminatus* and *A. nemoralis* were eliminated from over one half and more than ninety percent, respectively, of their modern ranges. The former may have survived in parts of the heterogeneous spruce forest of the southern Appalachians, and perhaps the adjacent Piedmont, particularly in association with red spruce. This habitat may have resembled those where this species is found today in the Appalachian Mountains and coastal New England/Maritimes. The extent of this 'refugium' is unknown, as is the exact location of ice-age refugia of most deciduous forest elements (Davis, 1976). The presence of fossil bogs on the continental shelf and in the Piedmont (Whitehead, 1972) indicates that suitable habitats existed that could have harbored *A. nemoralis* during that period. It may even have survived close to the ice edge in New Jersey, particularly if permafrost was negligible. Davis (1976) brings evidences of the probable survival of white pine and hemlock on the continental shelf.

From the terminal ice front position, deglaciation did not proceed as a uniform northward movement. In eastern North America, an ice lobe lingered over the Great Lakes, while ice was retreating rapidly along the eastern seaboard, from New England to Newfoundland. Much of the shelf was exposed still. Thus, by 12,000 yrs B.P. a wide corridor existed along the east coast, east of the St. Lawrence Valley (Ogden, 1977). Open spruce parkland already existed in New England and the Maritimes (Davis, 1976; Ogden, 1977).

It would not seem unreasonable to approximate the northward movement of closed boreal forest with a similar migration of *Aster nemoralis*, since their northern limits are correlated. One can envisage the following scenario. The dates used follow Davis (1976), Ogden (1977), and Richard (1977) (Figure 9).

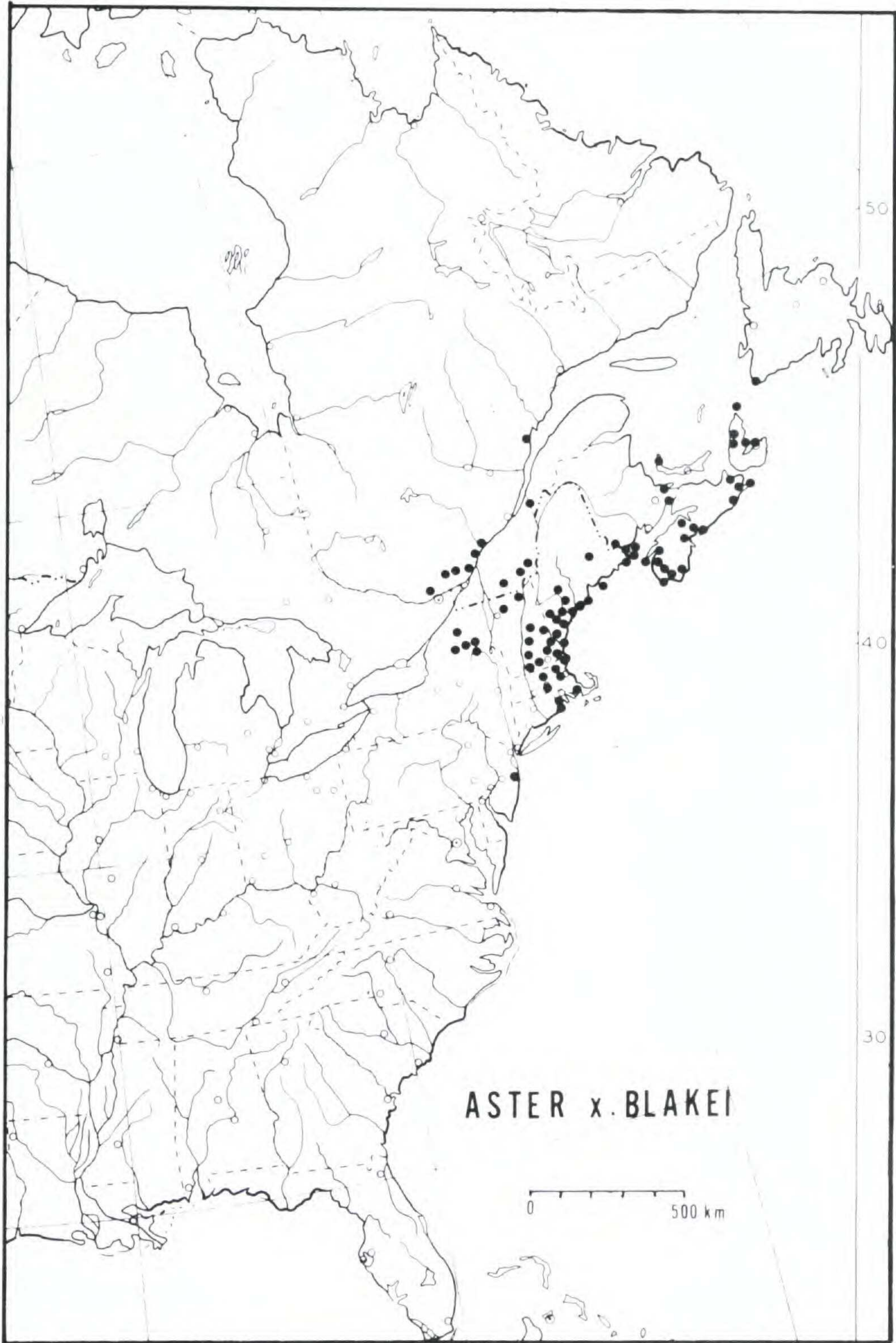


Figure 7. Distribution of Aster × blakei (Porter) House in eastern North America.

From its coastal plain-continental shelf "refugium", *Aster nemoralis* migrated northward through New Jersey and Long Island, spreading across bogs and pine barrens, mostly on the shelf. By about 11,500 yrs. B.P. It may have reached New England where the acidic substrate and the abundant pools were favorable to bog formation. At the same time, it would have taken a foothold in the maritimes, via the milder coastal route. Migration inland must have been slower due to proximity of ice. From Cape Breton Island (N.S.), this species was able to cross a then narrower Cabot Strait, probably in association with a number of boreal, bog (e.g. *Andromeda*, *Sarracenia*, etc.), and perhaps coastal plain (e.g. *Bartonia paniculata*, *Schizaea pusilla*) elements (Bouchard et al., 1978; Damman, 1965). This supposedly occurred between 11,000 and 9,000 yrs. B.P. Within the same time interval, it reached the Adirondack Mountains and southern Québec south-east of the Champlain Sea (Richard, 1977). From this position, migration may have followed this pattern: Laurentian Hills, ca. 8,500 years B.P.; Lac St-Jean area, 8,000 yrs. B.P.; Côte Nord, ca. 7,000 yrs. B.P. It ultimately reached its northern limit in the Churchill Falls area (Labrador) by ca. 5,000 yrs. B.P., the last remnant of ice having just melted in that region (ca. 6,000 yrs. B.P.) (Figure 9).

Northwestward expansion in northern Ontario is a different issue. *Aster nemoralis* may have reached the Algonquin highlands by about 8,000 yrs B.P., spreading afterwards toward the Districts of Muskoka, Parry Sound, and Sudbury. The lingering of an ice lobe over James Bay and the presence of lake Ojibway-Barlow delayed northward migration into Abitibi, eastern James Bay area (Québec), and northern Ontario. The first two areas may have been colonized by respectively 6,000 and 5,000 yrs. B.P. Westward migration from this front was probably blocked by the Tyrrell Sea and the high calcium levels of Hudson Bay Lowlands (see Fig. 6). Similarly, westward migration from Sudbury District was delayed by higher soil calcium content in glacial deposits north of Lake Huron (Baldwin, 1958). Moreover, we cannot use boreal forest progress as a yardstick of *A. nemoralis* migration, since elements of this formation may have come from the Upper Peninsula of Michigan as well as from the east. Thus *A. nemoralis* may have migrated in an area settled long before its arrival. Long-distance dispersal and chance establishment in suitable bogs west of the edaphic barrier are probably responsible for its establishment in the eastern Lake

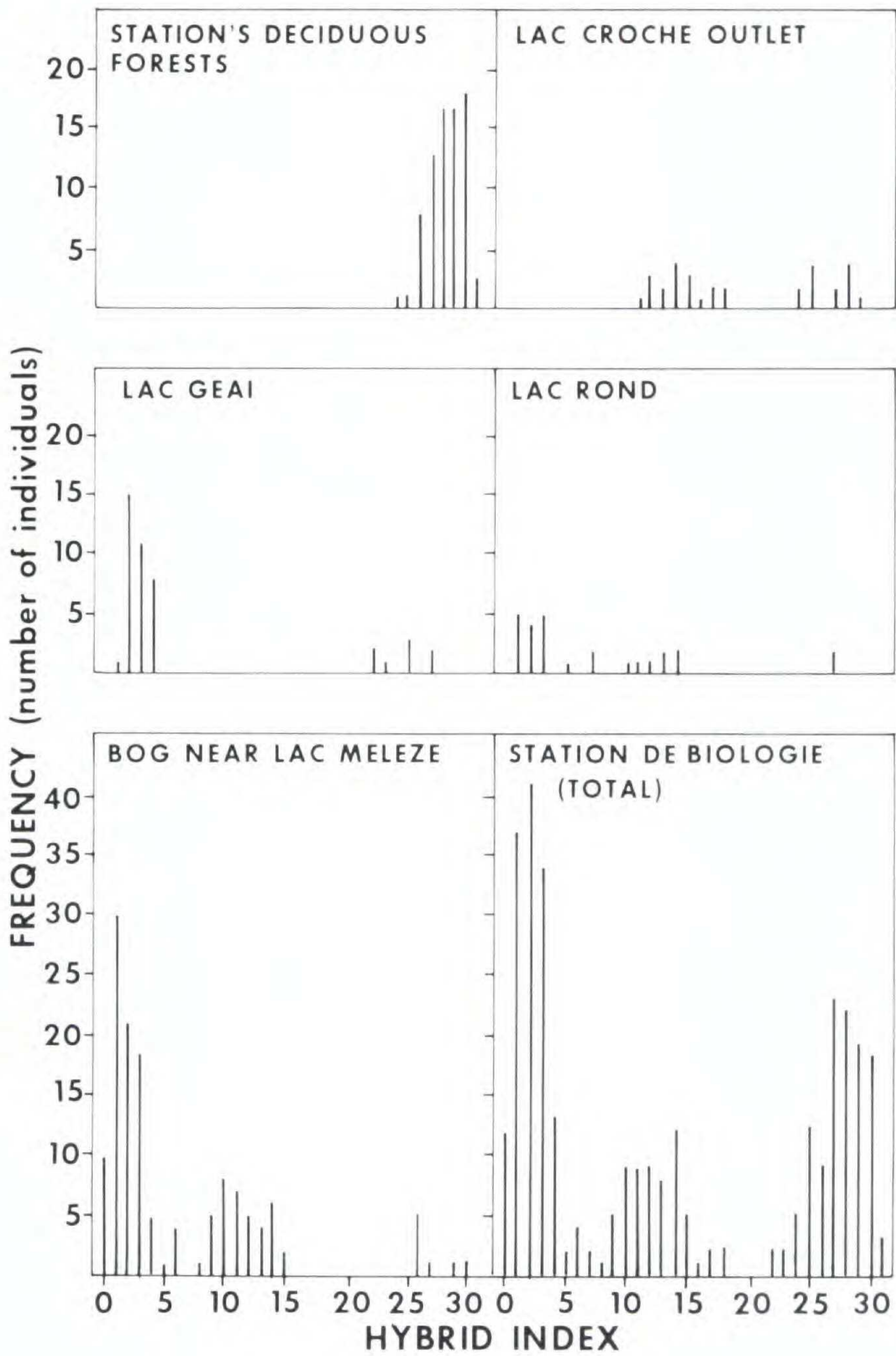


Figure 8. Frequency of individuals with different hybrid index (Pike, 1970) in many populations at the Station de Biologie, Université de Montréal, St. Hippolyte, Co. Terrebonne ($46^{\circ}00'N$, $76^{\circ}00'W$). Index range: *A. nemoralis*: 0-4; *A. × blakei*: 8-19; *A. acuminatus*: 25-31. Intermediate scores indicate backcrosses.

Superior area. This is rendered more likely by the existence today of disjunct populations on Caribou Island, in the middle of Lake Superior (Fig. 5), and in the Upper Peninsula (Mich.). The actual western limit may be a function of time and the species could still be expanding its range westward north of Lake Superior (Figure 9).

Migration of *Aster acuminatus* was probably delayed, in comparison to that of *A. nemoralis*, owing to its more southern refugium and its ecological requirements. The Appalachian highlands provided a first axis of migration. Upon reaching Pennsylvania-New Jersey, the spectrum of possible routes (Figure 9) broadened from the mountains to the shelf. At ca. 11,000 yrs. B.P., hardwoods started to replace boreal forest elements in this area and coastal New England (Davis, 1976). The establishment of yellow birch, with which this aster is often associated, could serve to estimate the pace of migration. However, this birch's pollen has not always been differentiated by palynologists and cannot be used extensively as yardstick. We have to use other temperate deciduous forest elements also. By 8,000 yrs. B.P., such elements were increasing in the Maritimes and southeastern Québec. This event may have corresponded with *A. acuminatus* arrival. From Cape Breton Island, it crossed the Cabot Strait to reach Newfoundland. A number of deciduous forest elements may have chosen the same route at roughly the same time, *inter alia* the yellow birch whose northern limit in Newfoundland is just to the north of *A. acuminatus*' northernmost locality on the island (Bouchard, et al., 1978). The Iles-de-la-Madeleine may have been reached also at this period, whether by long-distance dispersal or across a still partly exposed shelf. The Champlain Sea was no more a barrier when this species reached southern Québec. It may therefore have moved into the Laurentian Hills by 6,500 yrs. B.P., and Lac St-Jean area, its northern limit, by 5,000 yrs. B.P. The Gaspé Peninsula may have been colonized by plants coming from Maine and New Brunswick, as for the few *A. nemoralis* colonies (Figure 9).

The absence of westward expansion in eastern Ontario stresses the significance of the already discussed ecological barriers in this area. Certainly, time cannot be a factor here. The isolated Turkey Point (Ont.) population may represent a long-distance dispersal event or, alternatively, a relict from a period of range extension when climates were cooler and/or moister. A similar hypothesis is

used by Kapp (1977) to explain disjunct populations of hemlock west of its main range.

DISCUSSION

These two closely related perennial herbs display a close relationship between leaf characteristics and habitat. *Aster acuminatus* inhabits cool, mesic deciduous and mixed forests, and has a low number of wide-limbed leaves. In open, dry situations, the foliage is chlorotic, the blades narrower. The bog dweller, *A. nemoralis*, exhibits a great number of small, ericoid leaves of xerophytic character, an advantage in strongly insolated, nutritionally poor environments. *Aster acuminatus* has a distinctly Appalachian range, although it was successful in reaching the Laurentian Hills. Northern and southern limits correspond to isopleths of climatic parameters such as frost-free period and mean summer temperatures. The western limit is a result of the action of moisture and edaphic factors. On the other hand, *A. nemoralis* is confined to glaciated eastern North America, with the exception of the Pine Barrens of New Jersey. Acidity (or low levels of calcium) and conditions conducive to bog development play a prominent role in shaping its range. Both conditions are met on the acidic bedrock and pond-strewn landscape of the Canadian Shield and New England. Climatic factors (such as temperature) may delimit the southern edge of its range, since seemingly adequate environments exist further south on the Coastal Plain. Growing season and permafrost are likely determinant at the northern limit.

Thus, it appears that in both cases the factors controlling distribution at a local and regional level and those ruling over distribution at the continental level are similar. This phenomenon has been found in other studies (Bouchard & Maycock, 1970; Holland, 1974, 1975; Haber, 1977). In the case of *Viola rotundifolia* (Bouchard & Maycock, *loc. cit.*), an appalachian element, details of distribution are parallel to those of *A. acuminatus*. Examples are the hiatus in central Pennsylvania-Maryland, the southern limits in Georgia and east of the mountains. Discrepancies at the western and northern margins of the ranges underline differences in some of the ecological requirements of these species. However, major controlling factors are moisture and temperature in both cases.

That both regional and "continental" control are affected by the same factors is expected when the nature of adaptation is considered. Interactions of the milieu with a species' genome through selection produces adapted individuals. As this phenomenon operates at a local, populational level, it seems logical to infer that ultimate control over the range of a species will result from these same factors. Although ecotypic differentiation may appear to change ranges' outlines, it represents no more than a readjustment of distribution limits to slightly changed controlling parameters. Ecotypic variation is but a population phenomenon, and not a "cladogenetic" event (Quinn, 1978).

Many people may object to the use of correlations between climatic and/or edaphic parameters and distribution limits as a mean of detecting limiting factors. Their argument is that only an autoecological study is able to do so. Although it is true that ranges of tolerance to different factors can best be determined that way, there remains the problem of determining how these apply in nature, where other elements come into play, such as competition, diseases, etc. This is the classical potential vs. realized niche concept. Thus, biogeographical correlation still remains a valuable tool in this context, insofar as it only states the facts and does not try to infer direct causal relationships. Others would say, rightly, that range limits are not the result of single factors. However, it has repeatedly been noticed that isolated factors may have an overwhelming importance, determining *de facto* the level of reaction to other components (Dansereau, 1951). Jeffree (1955) has even shown that some species distributions can be modeled using a few temperature parameters. Furthermore, the use of different levels in analysis (local, regional, continental) ensures that the proper factors are selected. It thus seems reasonable to use correspondances between isopleths, or other geographically varying characteristics of the environment, and range limits as a first approximation of the nature and intensity of controlling factors. It will be the task of autecologists to determine their exact mode of action, be it direct or indirect. Biogeographical analysis and synthesis is after all a starting point.

In the second part, we tried to reconstruct post-glacial history of *Aster acuminatus* and *A. nemoralis*. As we pointed out earlier, the absence of fossils is handicapping our effort. The assumption that the ecological requirements of a species did not change from glacial

time to the Holocene is basic to such reconstitutions and deserves to be mentioned. It has been discussed by many paleoecologists with regard to paleoclimatological reconstructions. There is no way to prove that it is right or wrong.

A further point of concern is the location of the so-called "refugia". Very little information is available on this subject, particularly for eastern deciduous forest elements (Davis, 1976). The presence of macrofossils in deposits whose geographical location contrasts with present distribution stresses the problem of finding past ecogeographic equivalents of modern ranges (e.g. *Schizaea pusilla*, Whitehead, 1972; *Pinus banksiana*, Davis, 1976). The possibility of genetic depauperation, subsequent to population eradication by ice advance, and thus shrinkage of ranges of tolerance, has to be considered. Migration routes or fronts are also a facet of this problem (e.g. *Dryas integrifolia*, *D. drummondii*, Miller & Thompson, 1979). In our case, the shelf route can be postulated only because we know that fossils of plants and animals indicate their presence there during and after ice age (Flint, 1971; Ogden, 1977).

A careful application of our knowledge of present ecology and distribution of species, coupled with paleoecological reconstructions, are our chief means of historical analysis. A further element that can be used, with caution, is the glacial/post-glacial history of taxa whose fossil record is more complete and whose requirements and ranges overlap with those of the species under study.

Two points have to be taken into consideration: 1) differences in ecological requirements and life-form; 2) differences in dispersal potential. Let us use our utilization of yellow birch, *Betula alleghaniensis*, as a marker of *Aster acuminatus*' progression. Similarities and differences can be summarized as follows: a) the former species is a tree, the latter a perennial herb; b) yellow birch's range is wider to the west, and slightly so to the north; c) however, where they occur together their ecological needs seem to be similar in great part (both benefiting *inter alia* from small disturbances in the canopy for their establishment, etc.); and d) both are anemochorous. A taller individual can disperse propagules to greater mean distances owing to the higher starting point of its fruits. However, the shorter generation time of *A. acuminatus* may compensate for a smaller dispersion radius. The wider range implies that yellow birch is useful as an index only within the area where the whorled *Aster* is

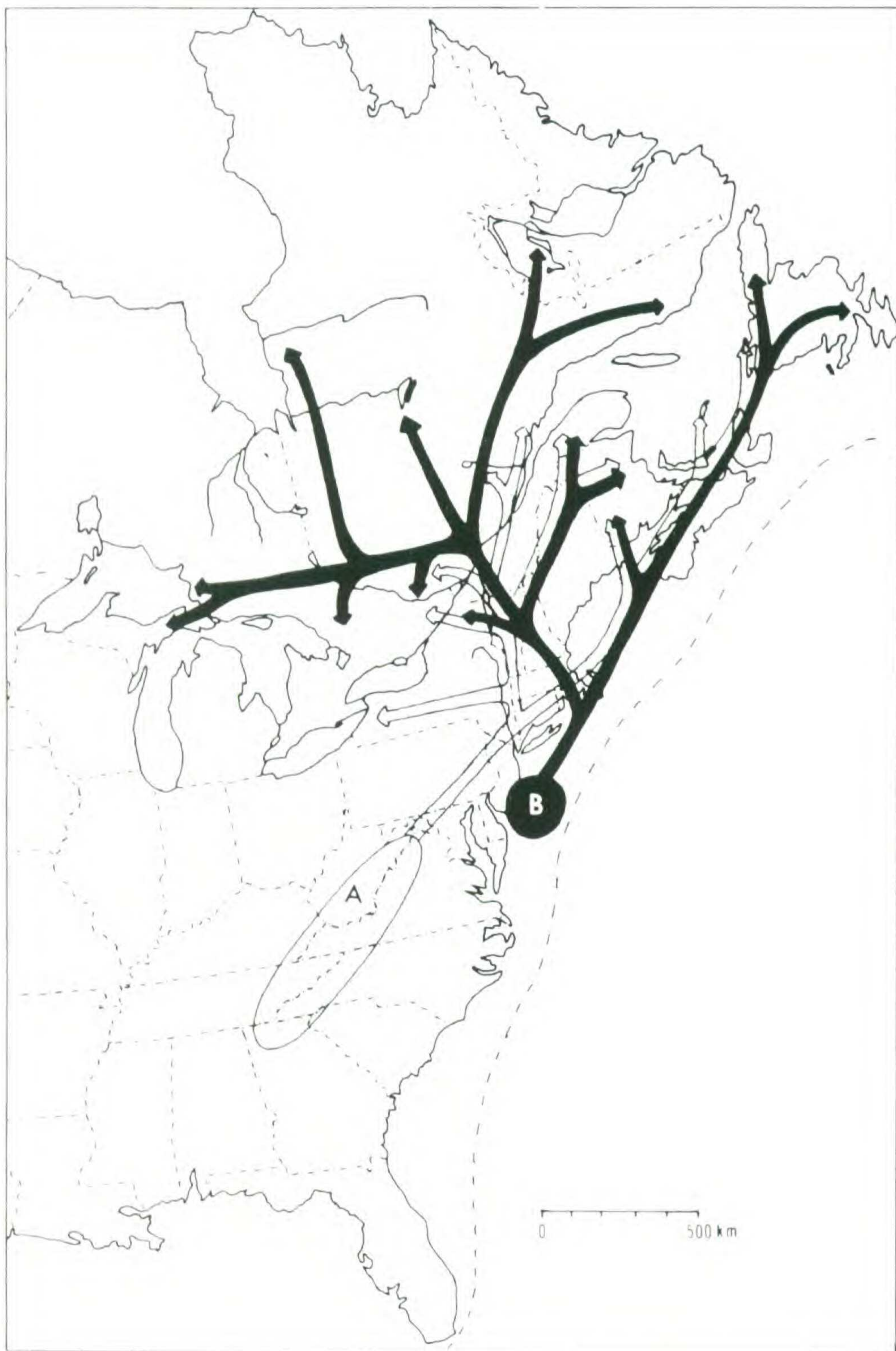


Figure 9. Probable Areas of Refugium, migration and recolonization routes of *Aster acuminatus* (A, grey) and *A. nemoralis* (B, black).

present today, i.e. in the eastern part of its range: the rest is irrelevant. Finally, the greater tolerance of the birch to northern conditions means that estimates of the *Aster* migration rate based on its progression will represent an upper limit, a maximum: *Aster acuminatus* may have been present in a given area not earlier than the date of yellow birch arrival. This short-coming could be alleviated by using a number of taxa of similar ecogeographies, which could provide a probability envelope. The same can be said of the use of vegetation units for this purpose, as we did with *A. nemoralis* and closed boreal forest. The application of such criteria is useful mostly in areas where revegetation sequence is parallel to present latitudinal zonation, i.e. where distortion of vegetation in the post-glacial was the least. Richard (1977) showed that this was the case for Québec, a region more remote from the ice front than New England where vegetation units were more intermingled (his "spring effect").

Hill (1976) postulated an introgression of genes from *Aster nemoralis* to *A. acuminatus* that would have occurred during the glaciation, in the Appalachians, to explain the aspect of individuals of *A. acuminatus* living on exposed summits of this region. His argument is based on two observations: 1) individuals of these populations tend to score lower than typical *A. acuminatus* when using Pike's index, due mostly to narrower leaves; 2) these plants show loose meiotic pairings and lower pollen fertility. Wells (1980) criticized Anderson-type indices because they tend to show evidences of hybridization even in cases where it is not occurring, reflecting author's biases in choosing the characters. Hill (*loc. cit.*) never considered the possibility of phenotypic plasticity. It has been observed by us that plants of this species exposed to drier, sunnier conditions have narrower, chlorotic leaves. Another possibility could be ecotypic adaptation. Furthermore, Jones (1976) demonstrates in experimental studies that pollen fertility in *Aster* is linked with the conditions under which a plant is grown: the greater the stress, the lesser the fertility. Loose pairing at metaphase I of meiosis (not an actual failure to pair) could also be ascribed to this phenomenon. Thirdly, there is no real support for the existence of *A. nemoralis* in the mountains. We do not reject, however, the possibility of hybridization on the Piedmont, where fossil bogs have been found. Finally, as we pointed out in the section on *Aster* × *blakei*'s distribution, hybridization in this case is definitely a local

phenomenon (Figure 8), which does not lead to extensive introgression even in sympatric areas. The selection gradient between bog and mesic forest seems to be strong enough to maintain genetic identity even in front of gene flow (May, et al., 1975). The dry, wind-and-sun-exposed summits mentioned by Hill (*loc. cit.*) are rather far, ecologically, from the ecotones where the hybrid grows. That its genes would be helpful in this context is far from proven!

This study encompasses several of the "integrative levels" of Dansereau (1951). The actual distributions of *Aster acuminatus* and *A. nemoralis* cannot tell us much about their phylogenetic history, since all their relatives (subgenus *Doellingeria*) are today restricted to eastern North America and no fossils are known. The paleobotanical level (level 1) was thus ignored. However, all the other levels (2 to 8) were involved: paleoecological, aerographical, bioclimatological and, in part, autoecological. We also used data from the synecological and phytosociological levels, particularly to determine controlling factors. Finally, the impact of man (land use and conservation) was also considered in due place. Thus, an ecogeographical analysis, based on a synthesis of all known data, certainly constitutes a source of useful information for the other plant scientists (taxonomists, ecologists, physiologists), as well as for the conservationist. There is certainly a need for more study of this type, particularly in relation to rare species' protection.

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